Tropical Ecology **54**(3): 301-308, 2013 ISSN 0564-3295

www.tropecol.com

The effects of ant attendance on aggregation of the honeydew producing lac insect *Kerria yunnanensis*

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Abstract: The relationship between some hemipterans and ants is generally thought to be mutualistic, as both partners seem to benefit from the association. Previous studies have shown that ant tending improves the survival and reproduction of hemipteran colonies, mainly by protection of hemipterans from enemy attack. However, the role of ant attendance in the presence of hemipteran enemies has rarely been addressed. In this paper, we investigated the biological features of the lac insect *Kerria yunnanensis* Ou et Hong in the presence of natural enemies. We found that *Crematogaster macaoensis* Wheeler attendance significantly decreased the amount of lac secreted by *K. yunnanensis*; both the amount of lac secreted by *K. yunnanensis* individuals and the thickness of lac secreted by the aggregation of *K. yunnanensis* under ant attendance were significantly smaller than those without *C. macaoensis* attendance. *C. macaoensis* attendance significantly benefits the aggregations of *K. yunnanensis*. Under *C. macaoensis* attendance, aggregations of *K. yunnanensis* had a higher survival rate, more females, and a larger number of offspring, when compared to aggregations not tended by ants.

Resumen: Generalmente se piensa que la relación entre algunos hemípteros y las hormigas es mutualista, ya que ambas partes parecen beneficiarse de la asociación. Estudios previos han demostrado que la asistencia de las hormiga mejora la supervivencia y la reproducción de las colonias de hemípteros, principalmente por la protección de los hemípteros del ataque enemigo. Sin embargo, pocas veces se ha analizado el papel de la asistencia de hormigas ante la presencia de los enemigos de los hemípteros. En este artículo investigamos las características biológicas del insecto de laca *Kerria yunnanensis* Ou et Hong en presencia de enemigos naturales. Encontramos que la asistencia de *Crematogaster macaoensis* Wheeler disminuyó significativamente la cantidad de laca secretada por *K. yunnanensis*; tanto la cantidad de laca secretada por individuos *K. yunnanensis* como el espesor de laca secretada por la congregación de *K. yunnanensis* con asistencia de hormiga fueron significativamente menores que los que no tuvieron asistencia de *C. macaoensis*. La asistencia de *C. macaoensis* benefició significativamente a las congregaciones de *K. yunnanensis*. Al contar con la asistencia de *C. macaoensis*, las congregaciones de *K. yunnanensis* tuvieron una tasa de supervivencia mayor, más hembras y un mayor número de crías, en comparación con las congregaciones no asistidas por hormigas.

Resumo: A relação entre alguns hemípteros e formigas geralmente é pensado ser mutualista, pois ambos os parceiros parecem beneficiar da associação. Estudos anteriores mostraram que a presença da formiga melhora a sobrevivência e reprodução das colónias de hemípteros, principalmente através da sua protecção ao ataque de inimigos. No entanto, o papel de presença de formigas na presença de inimigos dos hemípteros raramente tem sido abordado.

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Neste trabalho, investigou-se as características biológicas do inseto da laca *Kerria yunnanensis* Ou et Hong na presença de inimigos naturais. Descobrimos que a assistência da *Crematogaster macaoensis* Wheeler diminuiu significativamente a quantidade de laca segregada pela *K. yunnanensis*; tanto a quantidade de laca segregada pelos indivíduos de *K. yunnanensis*, como a espessura da laca segregada pela agregação de *K. yunnanensis* com a assistência das formigas foram significativamente menores do que sem a proteção da *C. macaoensis*. A assistência da *C. macaoensis* beneficiou significativamente as agregações de *K. yunnanensis*. Sob presença da *C. macaoensis*, as agregações de *K. yunnanensis* tiveram uma maior taxa de sobrevivência, mais fêmeas, e um maior número de descendentes, quando comparadas com as agregações não beneficiavam da presença das formigas.

Key words: Ant-attendance, biological feature, honeydew, lac insect, mutualism.

Introduction

Many species of hemipteran insects are mutualistically associated with ant species (Delabie 2001; Gullan 1997; Nixon 1951; Styrsky & Eubanks 2007). Tended hemipteran insects are generally assumed to be important food resources for many ant species, because their excretions contain energy-rich nutrients (Way 1963). Several studies have provided evidence that ants benefit from associations with hemipteran insects in terms of energy gain, which is thought to result in higher colony growth rates (Cushman & Beattie 1991; Degen *et al.* 1986; Fiedler & Maschwitz 1988; Pierce *et al.* 1987). In turn, ants often act as guards and decrease the impact of predators and parasitoids on the survival of the tended insects (Buckley 1987a; Cushman & Adicott 1989; Del-Claro & Oliveira 2000; Morales 2000; Way 1963). Mechanistically, ant-tended hemipterans may benefit from the removal of their honeydew, which reduces the mortality risk caused by fungal attack (Banks & Nixon 1958; Buckley 1987 a, b; Flatt & Weisser 2000; Renault *et al.* 2005; Skinner & Whittaker 1981). Ant tending may, therefore, considerably reduce mortality risks and thus provides a protection for hemipterans.

In experiments in which hemipteran colonies were reared in the presence and absence of ants, the ant mutualists beneficially affected biological features of the tended hemipterans in the absence of natural enemies. However, in nature, in the presence of ants, hemipteran colonies did not enjoy a completely enemy-free space (Addicott 1978; Bristow 1984; Cushman & Whitham 1989). So the positive effect of ant attendance on hemipterans may not be thoroughly ascribed to protection against natural enemies.

Lac insects live sessile lives on branches of the host plant. They produce lac, a layer of red resin on branches of host-trees on which they settle; in the adult stage, lac insects are thoroughly protected by lac crust. Lac resin is natural, biodegradable and non-toxic, and thus is widely used in food, textile and pharmaceutical industries in addition to surface coating, electrical component manufacturing, and other fields (Chen *et al.* 2010). Honeydew excreted by lac insects can be found on their bodies, or on the surfaces of leaves and branches, and can be seen as a by-product of their physiological processes.

In this paper, we assess the effects of attendance of the ant species *Crematogaster macaoensis* Wheeler on *Kerria yunnanensis* Ou et Hong, including the impacts on lac secretion and other biological features.

Materials and methods

Study system

This research was conducted in a lac insect agroecosystem in Mojiang county, Yunnan Province, in southwestern China (101º 43′ E, 23º 14′ N, 999.8 - 1056 m above sea level). The study site is characterized by an average annual rainfall of 1500 - 2100 mm (mostly in May to October) and a mean annual temperature of 18.2 ºC (observations in 2007 - 2010). The total area of the research plot was 10 ha. The lac insect agroecosystem is the main form of cultivation in mountainous regions between 900 - 1500 m a.s.l., with several lac insect host plant species distributed along or among the semi-arid agricultural plots. In this agroecosystem, the lac insect (*K. yunnanensis*) is cultivated by farmers on different parts of the host plant throughout the year, so the population is large. Sixty-four nests of *C. macaoensis* were found on *Dalbergia obtusifolia* Prain; the number of workers ranged from 5,000 to 80,000 per nest. *C. macaoensis* with other ant species visit *K. yunnanensis* for honeydew simultaneously. The honeydew is produced in surplus of the need of the ants, which leaves many droplets of honeydew uncollected. However, *C. macaoensis* can attend *K. yunnanensis* by constructing shelters on branches where *K. yunnanensis* has settled down or tend *K. yunnanensis* around the clock during the whole lifetime of *K. yunnanensis* by maintaining a large number of workers nearby its nest. In this experiment, eight-year-old *D. obtusifolia* with *K. yunnanensis* infestations were selected, ranging between 2.5 m to 2.8 m in height and between 5 cm to 7 cm in trunk diameter. The experiments were conducted from August 2009 to May 2010.

Experimental design

In August 2009, fifty *D. obtusfolia* individuals with similar height and trunk diameter were selected from the research area for an ant exclusion treatment. Before *K. yunnanensis* infesting on branches, the ants and ant nests were eliminated from the trees, and ants were prevented from visiting *K. yunnanensis* by coating sticky resin around the trunk of selected trees. The sticky resin belt was replaced every week, and also any bridge to the tree for ants was removed during the entire period of experiment. In the end of September, *K. yunnanensis* was cultivated on the selected plants.

In October, another fifty *D. obtusfolia* individuals with *C. macaoensis* attending *K. yunnanensis* were selected from the research area, to serve as an ant attendance treatment. To ensure the strength of ant attendance and that only one ant species was attending *K. yunnanensis*, only those *D. obtusfolia* plants meeting these criteria were selected: many workers visit *K. yunnanensis* day and night, no other ant species visits *K. yunnanensis* at any time, or shelters were constructed over *K. yunnanensis*, with several *C. macaoensis* workers in the shelter. Natural enemies of *K. yunnanensis* were not excluded from either of the two treatments.

Crematogaster macaoensis *attendance*

Ant activity is usually highly dynamic (in response to weather, colony needs, etc.), so the incidence of ants visiting *K. yunnanensis* was monitored throughout the whole life cycle of *K. yunnanensis* (from October 2009 to May 2010) to accurately characterize ant visitation of *K. yunnanensis*. The number of *C. macaoensis* on *K. yunnanensis* was investigated every month between 10:00 a.m. and 12:00 noon, 14:00 p.m. and 16:00 p.m.. Ultimately, twenty-one branches of *D. obtusfolia* with *K. yunnanensis* infestation were permanently attended by *C. macaoensis*. We selected 64 replicates on four branches as analysis data, where the length of lac crust was more than 10 cm. GLM were conducted to analyze the temporal variance of attending ant individuals by SPSS 16.0.

Investigation of predation and parasitism of K. yunnanensis *by natural enemies*

Assessment of predation of *K. yunnanensis* by natural enemies was conducted by counting holes in the lac crust (predators of lac insect usually enter the lac crust and eat lac insects and lac; at the same time, they eliminate dung through the hole where they entered into the lac crust). Parasitoids were collected from *K. yunnanensis* directly using cylindrical polyester mesh traps 25 cm in length × 10 cm in diameter (1 mm^2 mesh) that were placed for one month on branches where *K. yunnanensis* settled. The two ends of the mesh cylinder were fixed by a small iron wire, to prevent wasps from escaping. In the ant attendance treatment, twenty-one branches of *D. obtusfolia* with *K. yunnanensis* infestation which were permanently attended by *C. macaoensis* were selected. In the ant exclusion treatment, twenty-one branches of *D. obtusfolia* with *K. yunnanensis* infestation without *C. macaoensis* attendance were also selected.

Effect of ant attendance on K. yunnanensis *biological features*

Sex ratio

At the end of the larval stage, the sex of *K. yunnanensis* can be judged by the external characteristics of their lac crust (the lac crust of males is longer and slimmer than that of females). The sex ratios (here presented as the ratio of females to males) of *K. yunnanensis* per square centimeter were investigated on branches; 100 aggregations were sampled randomly, half of these from the ant attendance treatment, the other half from the ant exclusion treatment. All female-male ratios were log10 transformed, and the Levene statistic was applied to test homogeneity of variances; then a General Linear Model (GLM) was performed to compare the means of female-male ratios between ant attendance / ant exclusion treatments by SPSS 16.0.

Population survival rate

We investigated the population density of *K. yunnanensis* per square centimeter, at the first instar and adult stage. The survival rate is the percentage of *d2 / d1* (Chen *et al.* 2008), where, *d1* is the density of first instars, and *d2* is the density of adults. As with the previous experiment, a total of 100 aggregations were randomly sampled. Half of the aggregations were from the ant attendance experiment, the other half were from the ant exclusion experiment. All survival rates were log10 transformed, and the Levene statistic was applied to test homogeneity of variances, then GLM was performed to compare the means of survival rates between ant attendance / ant exclusion treatments by SPSS 16.0.

Amount of lac secreted and fecundity

At the end of the *K. yunnanensis* life cycle, before offspring emerged, lac crusts were collected and were cut into small pieces, with an area of 1 cm^2 for each piece. One hundred pieces of lac crust were selected randomly for study; half of the crusts were from ant attendance, the other half were from ant exclusion. Thickness of the lac crusts was measured by a vernier caliper. The Levene statistic was applied to test homogeneity of variances, and then GLM was performed to compare the means of lac crust thickness between ant attendance / ant exclusion treatments by SPSS 16.0.

Before measuring amount of lac secreted, the 100 lac crust pieces were checked carefully, and any lac crust that contained predators was excluded, as predators eat not only lac insects but also lac. Also, lac crust without continuous even thickness was excluded, because some adults died in their early stage. Ultimately, 71 pieces of lac crusts were selected, 31 from the ant attendance experiment, 40 from the ant exclusion experiment. The 71 pieces of lac crusts were weighed on an electronic balance (Sartorius BAS124S) one by one, and then each was put into a separate bottle with 95 % alcohol. One week later, after the lac was dissolved in alcohol, the female adults and other impurities in each bottle (such as wax, bark, etc.) were filtered out and were weighed on an electronic balance (Sartorius BAS124S) again. The number of adults was also counted. The amount of lac secreted by individual *K. yunnanensis* (mainly by adult females) was then counted as *(w1-w2)/ n*, where *w1* is the weight of lac crust, *w2* is the weight of female adults and other impurities, and *n* is the number of female adults (Chen *et al.* 2008). The data were log10 transformed, and the Levene statistic was applied to test homogeneity of variances, then GLM was performed to compare the means of the amount of lac secreted by *K. yunnanensis* individual between ant attendance / ant exclusion treatments by SPSS 16.0.

After weighing, the female adults from each treatment were mixed together, and one hundred gravid female adults (ensure embryos not have changed into larva) were selected randomly then, half from ant attendance, the other half from ant exclusion. Each selected female adult was dissected under a dissecting microscope (XTL - 2400), and the individual number of embryos in each female was counted. The Levene statistic was applied to test homogeneity of variances, and then GLM was performed to compare the means of offspring amount per female adult between ant attendance / ant exclusion treatments by SPSS 16.0.

Results

Crematogaster macaoensis *attend* K. yunnanensis

During the whole life history of *K. yunnanensis*, *C. macaoensis* permanently attended their lac insect mutualists 24 h a day. The number of ant workers on *K. yunnanensis* aggregations ranged from 19.12 ± 6.08/10 cm to 27.12 ± 6.42/10 cm. There was no temporal variation of individual numbers of *C. macaoensis* on *K. yunnanensis* aggregations during the entire study period (P = 0.249, F = 1.334, n = 64). There was also no temporal variation of individual numbers of *C. macaoensis* on *K. yunnanensis* aggregations during different time intervals in day and night observations (P = 0.324, F = 1.145, n = 273); the number of ant workers on *K. yunnanensis* aggregations ranged from 21.09 ± 8.62/10 cm to 27.76 ± 12.49/10 cm. Forty three shelters constructed by *C. macaoensis* were found over *K. yunnanensis*; the number of *C. macaoensis* inside the shelters ranged from 5 to 15, and no other ant species or arthropod was found in the shelters. Overall, *C. macaoensis* monopolized honeydew by attending *K. yunnanensis* with large number of workers day and night during the entire study period, or by constructing shelters over lac insects.

Effect of C. macaoensis *attendance on predation and parasitism of* K. yunnanensis

Crematogaster macaoensis attendance significantly reduced predation on *K. yunnanensis*. In

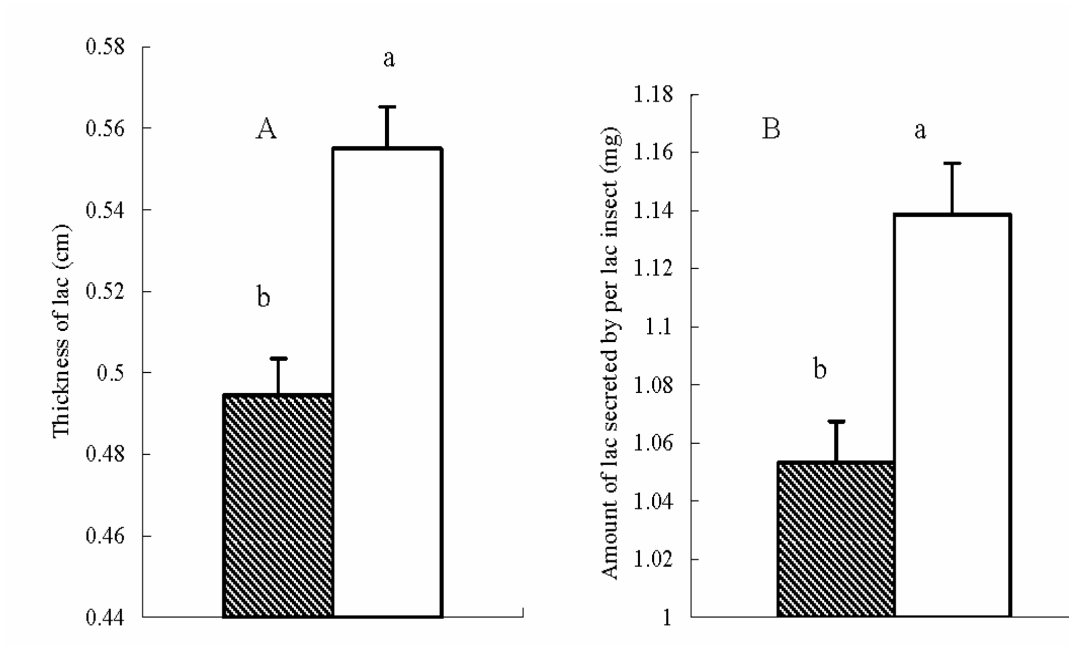

Fig. 1. The effect of *Crematogaster macaoensis* attendance on lac secretion of *Kerria yunnanensis*. Bars show means (± 1 standard error). Hatched bars represent ant-attended lac insects; open bars represent untended lac insects. (A) thickness of lac; (B) amount of lac secreted by one lac insect; Error line was added to the means. The significant difference defined at 0.05 levels is indicated by different letters.

the ant exclusion treatment, the mean density of *Holcocera pulverea* (the only predator we found) was 1.74 ± 0.22/100 cm^2, however, in the ant attendance treatment, the mean density of *Holcocera pulverea* was 0.00 ± 0.00/100 cm^2, suggested that *C. macaoensis* thoroughly controlled the predators of *K. yunnanensis*.

In terms of the effect of *C. macaoensis* on parasitism, ant attendance significantly reduced the population of *Tetrastichus purpureus* (the abundant parasite species collected from *K. yunnanensis* enclosed in fine polyester mesh). The density of *T. purpureus* within lac crust with ant attendance was 8.95 ± 2.50/30cm^2; the density of *T. purpureus* within lac crust was 87.36 ± 14.17/30 cm^2 in the ant exclusion treatment. However, ant attendance had no significant effect on *Tachardiae phagus tachardiae* populations and another parasitoid (Eulophidae sp.1).

Effect of C. macaoensis *attendance on amount of lac secreted by* K. yunnanensis

C. macaoensis attendance significantly reduced the production of lac secreted by *K. yunnanensis* (Fig. 1). The thickness of lac crust secreted by aggregations of *K. yunnanensis* with *C. macaoensis* attendance (0.4946 cm) was significantly smaller than that without ant attendance (0.555 cm) ($P < 0.0001$, $F = 19.956$, n = 71). In term of amount of lac secreted by *K. yunnanensis* individuals, *C. macaoensis* attendance significantly decreased this parameter, when compared to *K. yunnanensis* without ant attendance (before analysis, the data were log10 transformed, $P = 0.001$, $F = 13.28$, n = 100).

Effect of C. macaoensis *attendance on* K. yunnanensis *biological features*

Crematogaster macaoensis attendance significantly increased *K. yunnanensis* life history parameters, including female sex ratio, population survival rate, and the fecundity of adult females (Fig. 2). The female-male ratio of *K. yunnanensis* with *C. macaoensis* attendance was significantly higher than that without ant attendance (data were log10 transformed, $P < 0.0001$, $F = 117.723$, n = 100), which meant that there were more females in the ant-attended aggregations. The survival rate of populations with *C. macaoensis* attendance was significantly higher than that without ant attendance (data were log10 transformed, $P < 0.0001$, $F = 74.785$, n = 100), which meant that there

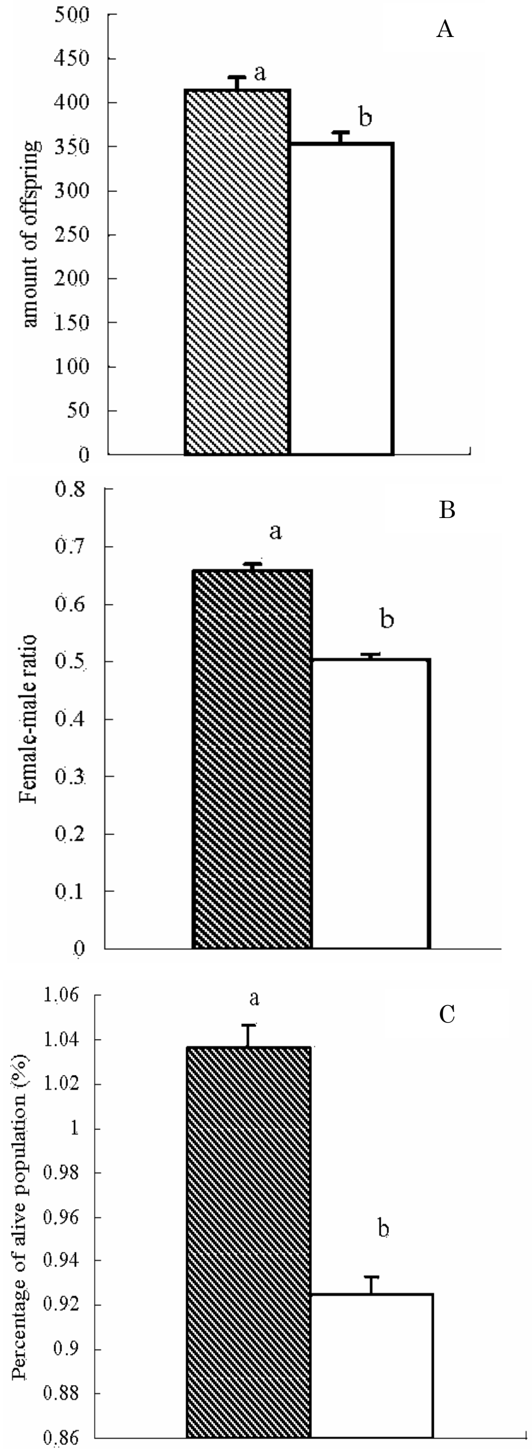

Fig. 2. The effect of *Crematogaster macaoensis* attendance on biological features of *Kerria yunnanensis*. Histograms show means (±1 standard error). Hatched bars represent ant-attended lac insects; open bars represent untended lac insects. (A) amount of offspring; (B) female-male ratio; (C) percentage of population alive. The significant difference defined at 0.05 levels is indicated by different letters.

were more adult females in the ant-attended aggregations (only for females that survived after mating). The fecundity of adult females of *K. yunnanensis* with *C. macaoensis* attendance (413.96 off-springs per female on average) was significantly higher than that without ant attendance (353.34 off-springs per female on average) (P = 0.003, F = 9.333, n = 100), which meant that there were more offspring in the ant-attended aggregations.

Discussion

The benefits of mutualism should ultimately be measured in terms of a direct fitness measure such as the survival rate of population and the number of offspring produced (Cushman & Beattie 1991; Del-Claro *et al.* 2006; Morales 2002; Rauch *et al.* 2002; Völkl *et al.* 1999). For lac insects, the present study is the first to follow aggregations throughout their life cycle, both in the presence of ant attendance and the absence of tending ants. In the field, in the presence of natural enemies, our study showed that *C. macaoensis* attendance positively affected all measures of lac insect fitness. Aggregations of *K. yunnanensis* attended by *C. macaoensis* survived on average 2.5 % more, had 6 % more females (male lac insects can mate with several females, the ratio of female to male is about 3:1, more females means more offspring will be produced), and had an expected number of offspring (referring to the number of offspring for each female) that was more than 17.0 % higher than individual females not tended by ants. These results are in accordance with previous studies showing that associations with ants can confer fitness benefits to tended hemipteran colonies (Banks & Nixon 1958; Bristow 1991; Buckley 1987 a, b; Stadler & Dixon 1999; Way 1963).

However, previous studies have found that the main benefit for hemipterans resulted from protection of colonies from natural enemies (Banks 1962; Banks & Macaulay 1967; Buckley 1987a, b; Stadler & Dixon 1998; Tilles & Wood 1982; Way 1963). Experiments conducted in the absence of natural enemies often failed to find a positive effect of ant tending on hemipteran reproduction or fecundity (Banks & Nixon 1958; Breton & Addicott 1992; Bristow 1984). In fact, in nature, in the presence of ants, hemipterans also suffered from natural enemies (Addicott 1978; Bristow 1984; Cushman & Whitham 1989). In our study, with around-the-clock attendance by many *C.*

macaoensis workers, *K. yunnanensis* also suffered parasitism. On the other hand, the damage due to predators had no effects on these selected biological features, for we only focused on the surviving *K. yunnanensis* aggregations, not the whole population, and some indices such as sex-ratio and fecundity of adult females were independent of natural enemies. Thus, the positive effect of ant attendance on hemipterans may not be thoroughly ascribed to a protection against natural enemies.

In this experiment, the selected hemipteran insect is *K. yunnanensis*, which can secrete lac to cover its body. Though the evidence for the function of different waxy secretions and protective coverings is largely circumstantial, depending on the type and amount of the secretion present it may protect scale insects against water loss, wet conditions, attack by natural enemies including pathogens, and contamination with their own honeydew (reviewed by Gullan & Kosztarab 1997), so lac could be defined as a kind of defence, which is costly for scale insects (Miller & Kosztarab 1979; Gullan & Kosztarab 1997). Chen & Wang (2006) reported that this defence decreased when alternative protection existed (the dense nylon web protecting lac insects against natural enemies during its whole life cycle). In this study, we documented that lac was relaxed and some indices of biological features were increased under ant attendance. We predict that ant attendance had positive effects on lac insect aggregation, mainly due to the decreased impact of natural enemies, at the same time, as an alternative defence of lac.

Acknowledgments

We wish to thank the farmers from the Mojiang County for giving permission to work on their properties. We also thank Dr. Xiaoyi Wu for his help on manuscript preparation in the English language. This research was partially supported by grants which were numbered as 201204602 and riricaf200801z.

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(Received on 12.07.2011 and accepted after revisions, on 28.05.2012)